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IS SEXUAL MONOMORPHISM A PREDICTOR OF POLYGYNANDRY? EVIDENCE FROM A SOCIAL MAMMAL, THE COLLARED PECCARY

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Running head: Genetic structure and parentage in collared peccaries

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Abstract

Sexual dimorphism is common in polygynous species, and there is clear evidence that both intra-sexual competition and female preferences can drive the evolution of large body size in males. In contrast, sexual monomorphism is often argued to reflect a relaxation of male mate competition or an intensification of resource competition among females. Alternatively, it might imply opportunities for females to circumvent or counteract male mate competition in a polygynandrous mating system. We test the prediction that sexual monorphism is associated with polygynandry in the collared peccary (*Pecari tajacu*, Tayassuidae), a social ungulate closely related to the old-world suids. The genetic mating system in the Tayassuidae is unknown, but its sexual monomorphism presents a striking contrast to the strong size dimorphism found in most Suidae, so that a departure from the polygynous system common in Suidae would be noteworthy. We characterized genetic relationships among adults within herds in three geographically distinct populations, assigned parents to 75 offspring, and tested for skew in individual reproductive success. Parentage assignment data indicated that multiple males sire offspring within a herd, and in the population for which genetic data were most complete, 19% of parentage assignments were potentially sired by extra-herd males. Some litters have multiple sires, and neither males nor females monopolized reproduction, even in small herds. This result supports our prediction and suggests that sexual monomorphism may either select for or be an evolutionary consequence of a promiscuous mating system.

Keywords: Artiodactyla, inbreeding, kinship, mate choice, multiple paternity, sociality

Introduction

Polygyny and polygynandry are both commonly observed among mammalian species (Greenwood 1980), including many species of ungulates (Jarman 1983). Classic mating system theory predicts that mate competition will drive the evolution of polygamy when access to the limiting sex is controllable (Emlen and Oring 1977), whereas the spatial dispersion and the cycle of sexual receptivity of the limiting sex will impose an upper bound on the ability of an individual to exploit this resource. The high incidence of polygamy among diverse taxa has been explained within this socioecological context (Emlen and Oring 1977), as have the secondary sexual characteristics (such as sexual dimorphism in body size) associated with intrasexual competition among males (Clutton-Brock *et al*. 1977; Perez-Barberia 2002) or sexual selection by females. Examples of morphological sex differences are so common in nature as to be the rule. There is abundant evidence to support the argument that mate competition and mate choice can contribute to significant reproductive variance among individuals, in turn promoting the evolution of secondary sexual traits (Andersson 1994), particularly large body size and elaborated weaponry in males.

However, in cases where the typical pattern of sexual dimorphism is absent or reversed, the selective pressures are less obvious. It is increasingly recognized that natural or sexual selection could act on females to influence the evolution of body size dimorphism (Clutton-Brock 2007; Gowaty 2005). The implications for the evolution of polygynandrous mating systems are profound, as sex reversals in body size dimorphism could limit the ability of males to control sexual access to females, creating an environment where females could mate with multiple males (Clutton-Brock and Parker

1995; Smuts and Smuts 1993). Conversely, opportunities for promiscuity or female mate choice based on traits other than male body size could counter selection for larger body size in males, leading to sexual monomorphism. It has been shown in the yellow pine chipmunk (*Tamius amoenus*) where sexual size dimorphism is biased toward females, that variation in reproductive success of both sexes is positively correlated with the number of mates (Schulte-Hostedde *et al.* 2004). The authors suggested that female multiple mating may be a characteristic of all species exhibiting sexual monomorphism or reversed size dimorphism.

Few studies have examined individual reproductive success in taxa with weak sexual size dimorphism (but see Vanpe *et al.* 2008). We examine this question using the collared peccary (*Pecari tajacu*, L), a species whose genetic mating system is unknown but whose sexual monomorphism contrasts markedly with the strong size dimorphism of related species and (based on tooth morphology of extinct and extant peccary species, Herring 1972; Wright 1993) is a trait that is recently derived.

Collared peccaries have been studied extensively with respect to behavior, ecology and taxonomy, yet until recently little was known about their population genetics (Cooper 2009, Cooper *et al* 2010; Theimer and Keim 1994) or genetic mating system. The species has successfully expanded its range into the southwestern United States, and is commonly found in Texas, New Mexico and Arizona (Sowls 1978). Several studies over the last 30 years suggest that the collared peccary exhibits interesting differences in social behavior and mating system when compared to other artiodactyls (even-toed ungulates) in general, and to the Suidae in particular.

Although the Artiodactyla exhibit a wide variety of social and mating systems, the suids (*Babyrousa, Potamochoerus, Porcula, Phacochoerus, Hylochoerus*, and *Sus*) are organized around single females and their young (Estes 1991). These females may periodically form social groups, termed sounders. Adult males either wander solitarily or in small bachelor groups (wild boar: Mauget *et al.*1984; warthogs: Somers *et al.* 1995), or they lead and protect a single-male harem wherein other adult and juvenile males are not tolerated (bushpigs and forest hogs, Estes 1991). The mating system of the Suidae is generally considered to be polygynous (Estes 1991) because aggressive male competition for mating opportunities is significant, and sexual dimorphism in body size or tusk size is marked. Conversely, all Tayassuidae (*Tayassu, Catagonus* and *Pecari*) are gregarious, living in stable, territorial herds with equal sex ratios that associate throughout the year (Bissonette 1982; Day 1985; Ellisor and Harwell 1979; Gabor and Hellgren 2000; Sowls 1997). There is little to no sexual dimorphism in body size (Lochmiller 1986, 1987), and both sexes are equally equipped with defensive weaponry in the form of long, sharp canine teeth. Behavioral evidence from studies on wild populations points to a more promiscuous mating system where male dominance or aggression may (Bissonette 1982) or may not (Byers and Bekoff 1981) confer a reproductive advantage. Studies of mating behavior in captive collared peccaries indicate that dominant males form consortships with estrous females (Packard *et al.* 1991), and tending of estrous females is common in nature (Bissonette 1982; Byers and Bekoff 1981). The role of female choice in mating behavior has not been directly addressed, although observational data indicate that females may either forcefully reject unsuitable males (Bissonette 1982; Byers and Bekoff 1981) or actively solicit matings (Byers and Bekoff 1981). It has been suggested that dominant males may enforce polygyny in smaller herds, but that larger herd sizes would prevent dominant males from sequestering multiple estrous females resulting in a more promiscuous system (Packard *et al.* 1991).

Here we test the hypothesis that sexual monomorphism in body size can predict a polygynandrous mating system in the collared peccary, where resource defense polygyny might be expected. We use multi-locus microsatellite data to genotype individuals within herds sampled from three Texas populations. We use these genotype data to describe genetic relatedness and familial relationships within herds, perform parentage analyses, and test for a signal of reproductive skew for both sexes, in order to assess whether patterns are consistent with a polygynous or a polygynandrous mating system in this sexually monomorphic species.

Materials and Methods

Sampling

We genetically sampled three populations of collared peccaries in Texas (Figure 1). During 1995-1998, blood samples were collected from live-trapped animals in the Chaparral Wildlife Management Area (CWMA) in south Texas (see Gabor and Hellgren 2000 for methods). During 2004-2006 we collected tissue samples from live-trapped animals in the Welder Wildlife Refuge (WWR) on the Gulf Coast and in Big Bend Ranch State Park (BB) in the Trans-Pecos Region. Each sample was collected from an individually marked, live-trapped individual, with associated data on age, sex, herd affiliation and territory location.

To collect tissue samples at the Welder Wildlife Refuge and Big Bend Ranch State Park we trapped collared peccary herds in corrals (5 m^2) constructed from 10 x 10 cm wire mesh panels. The entrance to the corral also served as the handling chute, and was constructed out of wire mesh welded to a steel frame. This chute was open at the top for handling access, with a swinging gate at the front and rear. We constructed traps in areas of high peccary usage (evaluated from feeding sign, fresh feces, bedding sites and remote camera data) and baited them with dried feed corn. Prior to trapping we allowed for a period of habituation to maximize the probability of trapping entire herds. Remote infra-red wildlife cameras (Stealth Cam, Grand Prairie, TX) were placed near traps to collect information on herd numbers and age classes. Traps were set when camera data indicated that all herd members were consistently entering the enclosures; usually two or three trapping sessions sufficed to sample all known individuals.

Summer trapping sessions were conducted at night to minimize heat stress. Once a trapping session was initiated by a hidden observer pulling the cord attached to the manual trigger, we quickly covered the wire mesh corral “walls” with plastic tarps. Once the tarps were in place, individuals became calm enough to respond to workers directing them one at a time into the handling chute. When an individual entered the chute, we closed and fastened the rear door, separating the focal animal from herd members in the corral. We determined the sex of the individual, and estimated by eye the age based on behavior, morphological traits and weight class. Individuals with an estimated weight of <6 kg and exhibiting immature characteristics such as ginger pelage, undescended testicles and adult-oriented following behavior were classed as infants. Individuals with an estimated weight of 6-11 kg were classed as juveniles. Infants and juveniles are collectively referred to as immatures. Animals with an estimated weight of

>11 kg were classed as adults, based on genetic estimates of dispersal age (Cooper *et al.* 2010). We then used the swinging front gate, coupled with a heavy plywood board, to restrain the subject against the wall of the box. We collected a 2 mm^2 tissue sample using a pig ear punch, and inserted a uniquely numbered button ear tag (colors corresponded with herds). Tissue samples were stored in lysis buffer (100mM Tris-Cl pH 8, 10mM EDTA, 1% SDS, ddH2O) until DNA was extracted for long-term storage at 4C.

Genetic analysis

We isolated *P. tajacu* genomic DNA from blood and tissue following methods outlined in Cooper *et al.* (2010). Using previously described cloning methods (Glenn and Schable 2005; Hamilton *et al.* 1999; Williams and DeWoody 2004) we characterized six novel microsatellite sequences from a genomic library (Cooper 2009). We ultimately amplified *P. tajacu* genomic DNA with a combined suite of 11 microsatellite markers, using domestic pig primers (Alexander *et al.* 1996; Archibald *et al.* 1995; Ellegren *et al.* 1994; Rohrer *et al.* 1994; for other cross-amplification efforts see Gongora *et al.* 2002; Lowden *et al.* 2002) and *P. tajacu* primers. We also utilized 7 mtDNA haplotypes based on d-loop sequence variation (Cooper *et al.* 2010) for parentage analysis.

Genetic structure within herds

We used the program ML Relate (Kalinowski *et al.* 2006) to calculate pairwise estimates of genetic relatedness and assign pedigree relationships within herds. We used the Monte Carlo randomization method within ML Relate to test for departures from HWE, and then specified which loci departed from equilibrium. ML Relate calculates maximum likelihood estimates of relatedness (*r*) from multi-locus microsatellite genotypes, and calculates the likelihoods that two members of a pair are unrelated, half-siblings, full siblings or parent-offspring pairs. All relationships were subjected to a likelihood ratio hypothesis test (over 10,000 simulations at 95% confidence), against the likelihood of an alternative relationship. When the putative relationship was parent-offspring (PO), the alternative hypothesized relationship was full-sib (FS); when the putative relationship was full-sib, then the alternative was half-sib (HS); and when the putative relationship was unrelated (U), the alternative was half-sib. If significance was reached in multiple tests, then we accepted the closer familial relationship as most likely. For example, if the likelihood ratio test for FS vs. HS yielded a significant result, and the test was also significant for HS vs. U, then we accepted full siblings as the most likely relationship. If the first test (FS vs. HS) was not significant, but the second test (HS vs. U) was, then we accepted half siblings as the most likely relationship. Misassignment of close kin using Queller and Goodnight's (1989) estimator of relatedness (as used in ML Relate) can be substantial, resulting in an inferred pedigree which exaggerates consanguinity (Van Horn *et al.* 2008). We therefore assessed the discriminatory power of this estimator for this marker set by calculating the proportion of tests that distinguished relationship categories (e.g. PO vs. FS) at a significance level of 0.05.

Parentage

Parentage analyses were performed for 99 immatures (and one individual of indeterminate age class) using CERVUS 3.0.3 (Kalinowski *et al.* 2007). We tested for departures from HWE and removed loci with null allele frequencies greater than 0.10. We performed sequential CERVUS analyses for each population, assigning trios at 95% confidence when possible, and accepting single parental assignments at 95%

confidence when both parents could not be assigned. A single allelic mismatch was allowed between parents and offspring or within a trio. We compared mtDNA d-loop haplotype assignments (Cooper *et al.* 2010) between offspring and all putative mothers, and restricted the set of candidate mothers to adult females that shared a haplotype with the offspring being considered. We began with the most parsimonious expectation for parentage: we only considered adults within the herd to be candidate mothers or sires. When we could not find a trio at 95% confidence, we searched for a mother or a father at 95% confidence. When we could not find a parent within the herd, we broadened our search to consider as candidate sires adult males in herds within 5 km (Bowman *et al.* 2002) of the herd under consideration. Extra-herd males were accepted as sires only when they met the 95% confidence criterion (and no resident male had a high enough LOD score to meet the criterion). When presented with a case where both a candidate mother (within the herd) and father (within the herd or extra-herd) were assigned singly at 95% confidence, but failed to be assigned as a trio at 95% confidence, then we accepted the maternal assignment only. In the single case where we were searching for the parentage of an individual of indeterminate age class (who could have already dispersed), we expanded the search to include females in herds within 5 km.

To assess the incidence of consanguineous mating between the Cervus-defined parents, we used ML Relate to calculate the log-likelihood ratios of four possible relationships (U, HS, FS, PO). We then performed three sequential likelihood ratio hypothesis tests (α = 0.05) for each pair of parents, with the putative relationship specified as the relationship with the highest log-likelihood value, and the alternative relationship specified as any of the 3 remaining possible relationships.

Reproductive skew

We tested for the presence of reproductive skew in adult males and in adult females using the program Skew Calculator 2003 1.2 (Nonacs 2000). This program calculates the binomial skew index (B), which is the observed minus the expected variance in reproductive skew, under a normalized null expectation that all individuals within a group (weighted for group size) have an equal probability of gaining benefits (in this case, producing offspring). B takes a negative value when reproduction is more evenly distributed than expected, a positive value when skew is greater than expected, and a value of zero when reproduction is randomly distributed. We calculated B separately for both male and female adult individuals within herds. Benefits included all offspring attributed to each individual, whether the offspring was within that herd or resident in another herd. Time in the group was held constant for all individuals. Significance was assessed over 10,000 simulations and confidence intervals were calculated with $\alpha = 0.05$. If the confidence intervals calculated using Skew Calculator include zero, then random sharing of benefits cannot be excluded as an explanation for the observed B value. If the lower confidence interval includes the equal sharing value (the minimum B value possible if benefits are equally shared among all group members), then an equal distribution of benefits cannot be excluded. If the upper confidence interval includes the monopoly value (the maximum B value possible if all benefits accrue to a single group member), then total monopoly by one individual cannot be excluded. The power to detect reproductive skew was assessed via simulation of B values, over 5000 simulated herds ranging in size from one to 100. This approach calculates the probability that the mean B value of a group of any particular size will exceed zero, where P is the probability that the observed degree of skew exceeds random with a one-tailed test given the observed herd sizes and offspring assignments.

Results

We captured 203 individuals from 20 herds within the CWMA population over a three-year period (some individuals were trapped multiple times). Genetic samples were collected for only some of the subjects, resulting in genotypes for 102 individuals (50%) derived from 16 herds. Ten of these 16 herds contained immatures. A more complete sample was achieved for the BB population (92.5% of individuals observed), with 135 captures from 13 herds and all captured individuals genotyped. We captured 31 individuals from four herds in the WWR population, and genotyped all individuals. Herds ranged in size from two to 18 animals, and mean herd size over all three populations was 8.9 animals (for a demographic summary, see Cooper *et al.* 2010).

Individuals were genotyped at 11 polymorphic microsatellite loci. Although we were not able to obtain complete genotypes for every single individual at every locus because of unsuccessful amplification, the number of individuals typed (the mean proportion over all loci) was substantial (Table 1). When tested for departures from HWE, two loci exhibited null alleles (JCIFG1 in BB, S0113 in CWMA) and were removed from the Cervus parentage analyses. Allelic diversity among the remaining loci was moderate (Table 1), with means ranging from 5.6 to 6.2 alleles per locus.

Genetic structure within herds

The mean relatedness among adult females within a herd was high (Table 2), approximating that expected among half sibs (i.e. 0.25). Surprisingly, the mean relatedness among adult males within a herd was also high. In the BB and CWMA populations combined (WWR was excluded because of small sample size), there was no significant difference (t = 0.86, df = 148, p = 0.39) between mean relatedness within herds in males (0.22 ± 0.02) and females (0.24 ± 0.02). When separated by population, mean relatedness among females (BB = 0.26 ± 0.03, CWMA = 0.22 ± 0.02) and males (BB = 0.25 ± 0.02, CWMA = 0.18 ± 0.02) did not differ significantly (BB: t = 0.15, df = 80, p = 0.88; CWMA: t = 1.37, df = 66, p = 0.17).

To examine within-herd relatedness in more detail, we investigated the frequencies of specific close kin relationships among adult males, among adult females and between sexes. An estimate of the discriminatory power of our marker set is provided by the proportion of tests that distinguished parent/offspring from full-sib (18/47 = 38%), full-sib from half-sib (18/34 = 53%) and half-sib from unrelated (16/70 = 23%) at α = 0.05. Results suggest that in the BB population, 42% of the 45 adult males had an apparent father or adult son among herd members, 36% had one or more full brothers in their herd, and 67% had at least one half-brother. However, 38% of adult males had to contend with one or more unrelated resident adult males. Stated another way, the average adult male had 0.9 fathers or adult sons in his herd; Table 2 also summarizes the number of brothers and unrelated male herdmates for the average adult male.

Of the 37 adult females within the BB population, 32% lived with an adult female which was likely their mother or daughter. Adult females had on average 1.7 mothers or adult daughters in their herd Adult females exhibited a pattern that was almost identical to males when same-sex full siblings were considered, with 35% sharing herd membership with an adult full sister. However, herds also contained a non-trivial number of apparently unrelated adult females (Table 2).

Mean relatedness between females and males within herds was substantial (BB = 0.21 ± 0.02, CWMA = 0.19 ± 0.02), and there was no significant difference between population means ($t = 1.04$, $df = 69$, $p = 0.30$). Most breeding-age females (BB, 68%; CWMA, 59%) had at least one male within their herd with whom they shared an r of > 0.10. Some males exhibited pairwise r values of zero with every adult female within their herd, with the exception of one or two females with whom they shared a pairwise r of 0.50 (±0.01).

While most related male herd-mates were probably still in their natal herds, there were three cases of apparent post-dispersal male relatives (two likely father/son pairs and one pair of likely full brothers) living in the same herd. This phenomenon was evidenced by a very low mean relatedness between these post-dispersal males and female residents (0.02), compared to a substantial mean r between putative natal resident males and female natal residents (0.33).

Parentage

Across all three populations, our maternal assignment rate was 55%, our paternal assignment rate was 52%, and 30% of immature animals were assigned both a mother and a father (Table 1). Parentage assignment rates were highest for the BB population because of the more complete sampling, with 42% of offspring assigned only one parent and 54% of offspring assigned both parents. Within the CWMA population, where 50% of the herd members were genetically sampled, 55% of offspring were assigned one parent and 9% were assigned both. Parental assignment rates were the lowest in the WWR population, where many parental and offspring genotypes were incomplete. Only one mother and one father could be assigned with 95% certainty.

Of the 31 herds sampled across three populations, 23 contained >1 adult male, and paternity was assigned to more than a single adult male within 10 herds (43%). This is surely an underestimate, as many paternity assignments in the WWR and CWMA populations could not be made because the sire was not genetically sampled. In the most completely sampled population (BB), paternity was assigned to more than one male in 5 out of 6 multi-male herds (83%).

Our results suggest that males sire offspring in herds with which they are not currently associated. For example, 7/37 progeny (19%) in BB were apparently sired by males in another herd. Of these extra-herd assignments, five were attributed to two males in herds sharing a territorial boundary with the offspring's natal herd (Arroyo/Monte, Liebre/La Posta). One of these males mated twice with the same female, producing three offspring, and the other male mated with two females in the adjacent herd, producing a single offspring with each. Similarly, 5/13 (38%) of progeny in CWMA were apparently sired by extragroup males, although these assignments are less certain because not all group males were genotyped in this population.

In BB, we estimated an error rate associated with extra-herd paternity assignments by searching for extra-herd mothers (within 5km) for the 11 offspring that were not assigned mothers. Our assumption was that immature individuals should still be living in the same herd as their true mother; if an offspring was therefore assigned an extra-herd mother at 95% confidence, we considered this an error. We found an apparent extra-herd "mother" for only 1/11 (9%) of these immatures.

Likelihood ratio tests indicated that three of the 25 offspring assigned both parents in the BB population resulted from matings between probable half-siblings (Table 3), one mating occurred between two full siblings, and two matings occurred between an assigned parent and offspring (PO). The PO matings occurred between the same pair of individuals (resulting in a singleton and a set of two littermates), and the male was not currently associated with the herd.

We looked for littermates among immatures (the only age class for which we could confidently estimate birth season) in the BB and CWMA populations by determining those infants assigned to the same mother. We identified six litters (five sibling pairs and one sibling trio); within two litters the siblings were assigned to different sires, and within the litter of three, two offspring were full siblings and the third sibling was assigned a different sire.

Reproductive skew

We estimated reproductive skew for adult males in the six herds in the BB population for which >1 offspring were assigned sires (Table 4). Across all six herds, there was no clear evidence for reproductive skew (mean B = 0.06, range: -0.06 to 0.33, $p = 0.14$). However, in only 5 cases (3 tests for females, 2 tests for males) were the herd sizes large enough to detect a signal of reproductive skew if it were present ($p<0.05$). Of these cases, two tests for females (Arroyo and La Posta herds) and one test for males (Liebre herd) yielded positive B values, but the confidence intervals included the equal sharing values, zero, and the monopoly values, indicating that all available explanations for reproductive benefits (equal sharing, random, or monopoly) were possible. One test for females (Monte herd) yielded a negative B value (-0.22) and the 95% CI did not include the monopoly value, which suggested that reproduction was either equally shared among female herd members, or randomly shared. One test for males (Arroyo herd) resulted in a positive B value (B = 0.14) and the confidence interval did not include the monopoly value, suggesting that reproduction may be positively skewed in this herd (four of the seven offspring were attributed to a single sire), However, the confidence interval included zero, indicating that this herd did not exhibit a significant difference from random sharing of reproduction.

Discussion

Genetic structure within herds

These microsatellite-based analyses of within-herd relatedness indicate that collared peccary herds comprise a mixture of female and male adult relatives and non-relatives. Given that collared peccaries live for approximately 10 years, conceive at 17 months (Hellgren *et al.* 1995) and exhibit an inter-birth interval of approximately one year (Sowls 1978), it is probable that herds comprise both male and female lineages spanning multiple generations. We found that within-herd relatedness among males did not differ from that among females, a result that is congruent with isolation-by-distance estimates (Cooper 2009). Our results point to a moderate level of female dispersal, which clarifies our understanding of mtDNA haplotype admixture (Cooper *et al.* 2010). Pairwise comparisons of relatedness among herd residents indicate that some adult males found with likely male relatives are post-dispersers, suggesting that these individuals either disperse together or preferentially disperse into herds with familiar males. Our data suggest that some individuals remain as adults in their natal herds. Natal philopatry may be selectively favored by cooperation with herd members, and these benefits would be amplified indirectly via cooperation with relatives (Dobson *et al.* 1998; Hamilton 1964; Silk 2002; Trivers 1971). Collared peccaries exhibit high rates of affiliative behaviors (Bissonette 1982; Byers and Bekoff 1981; Sowls 1974) and “altruistic” behaviors such as allo-nursing (a female nursing another's offspring), food sharing and cooperative defense (Babbitt and Packard 1990; Byers and Bekoff 1981). The evidence presented here suggests that the potential exists for adults of both sexes to engage in support behaviors with same-sex relatives in competitive interactions (Olson and Blumstein 2009).

Parentage and mating system

This species exhibits a more promiscuous mating system than behavioral data suggest (Bissonette 1982; Packard *et al.* 1991), as commonly happens in molecular studies of parentage (Griffith *et al.* 2002; Tregenza and Wedell 2000), including that of wild *Sus scrofa* (Poteaux *et al.* 2009). Three lines of evidence indicate that the mating system in *P. tajacu* is polygynandrous. First, most herds within the BB and CWMA populations contained immature individuals sired by different resident males. Second, there was evidence for multiple paternity within litters. Third, there was no evidence for male or female reproductive skew in the BB population, irrespective of herd size. Our power of detecting reproductive skew is limited by small herd sizes (Dugdale *et al.* 2008), but in those cases where statistical power was high results are consistent with the possibility that reproduction is distributed either randomly among breeding individuals, or more equally than expected under the null (binomial) distribution.

These data, suggest that either dominant males are unable to sequester or monopolize estrous females, or that female choice (overt or cryptic) plays a role in mating behavior. Untended estrous females ranging along territorial boundaries might encounter opportunities to mate with males from another herd. Post-mating copulatory plugs have been observed in this species (Hellgren 1989; Packard *et al*. 1991). There is evidence that copulatory plugs are negatively associated with degree of sexual dimorphism and females' sexual receptivity length, indicating that passive mate guarding with copulatory plugs can be a successful alternative strategy to active guarding and agonistic competition (Dunham and Rudolf 2009). The sexual receptive period in female collared peccaries is short (from two to four days; Lochmiller *et al.* 1984; Mauget *et al.* 1997) suggesting that males could have evolved a response to female promiscuity.

Promiscuous mating within a single breeding season can lead to multiple paternity within a single litter. We found evidence for multiple paternity within 3 out of 6 litters (50%). Wolff and Macdonald (2004) proposed several explanations for multiple mating in mammals, and several are relevant for *P. tajacu*. It is possible that promiscuous mating has evolved as an anti-infanticide strategy, or as a bet-hedging strategy against male infertility or genetic incompatibility. It has been demonstrated that promiscuous species have lower rates of early reproductive failure than monogamous and polygynous species (Stockley 2003). Multiple mating can also serve to increase genetic diversity (Wolff and Macdonald 2004), which would be advantageous in a stochastic environment or, as in the case of *P. tajacu*, the species is rapidly expanding its distribution into novel environments. It has also been suggested that multiple mating allows postcopulation sexual selection through sperm competition to occur (Wolff and Macdonald 2004). Females may exercise cryptic mate choice through differential sequestration and expenditure of sperm, or selection may be favoring males whose sperm is most competitive; this second explanation is persuasive given that copulatory plugs have been observed in collared peccaries

We found that occasionally females mated with and produced offspring with likely male relatives. Five out of the 25 trio parentage assignments made for the BB population were the result of breeding with a relative. Of the three females exhibiting multiple paternity within a single litter, two had engaged in both a consanguineous and an unrelated mating. However, pairwise comparisons of mean *r* among breeding-age adults within herds clearly indicate that most females have access to an unrelated male for mating opportunities. It is not clear what rules females may use with regard to mate choice and inbreeding avoidance, and published data point to a lack of olfactory-based kin recognition in the suids (Puppe 1998, Stookey and Gonyou 1998). It does not appear that females are avoiding copulations with males they matured with, because all of the putative inbred matings (except two parent-offspring/full sibling unions) were with resident males who had not dispersed.

Several explanations for the evolution of sexual monomorphism in *P. tajacu* are viable. Selection for large body size irrespective of sex may result from the herd defensive behaviors exhibited by *P. tajacu* toward conspecifics (during territorial encounters) and toward predators. Observations of wild populations (Bissonette 1982; Byers and Bekoff 1981) include significant aggression displayed toward other herds at territorial boundaries, as well as coordinated responses toward predators. No sex-specific difference in behavior has been reported. It is possible that there exists equal selective pressure on both sexes for defensive armament such as large canines and heavy shoulders to maintain these traits in the absence of sexual selection.

A second explanation for the evolution of sexual monomorphism in *P. tajacu* is increased selective pressure on females for large body size to aid in aggressive dominance interactions over food. There is evidence that body condition, including body mass, is positively correlated with fecundity (Hellgren *et al.* 1995). However, food competition among female collared peccaries is not aggressive, and female dominance status and body size do not heavily influence the outcome of such interactions (Bissonette 1982).

Lastly, selective pressure on males for large body size which is associated with aggressive intra-sexual mate competition may be relaxed, because the trait does not translate into increased reproductive success. Dominance interactions among male collared peccaries may play a significant role in mating, but body size may not strongly influence dominance status, although it has been demonstrated that body size and social rank can be associated with serum testosterone levels (Hellgren *et al*. 1989). However, rank may be of such a short duration as to have little effect on reproductive skew across breeding seasons. Conversely, female mate choice may be based on traits other than body size, reducing any selective advantage to larger males and increasing the likelihood that smaller males reproduce. In wild *Sus scrofa*, some variation exists among populations with respect to the degree of polygyny and multiple paternity observed (Delgado *et al.* 2008; Hampton *et al.* 2004; Poteaux *et al.* 2009; Spencer *et al.*

2005). Although large *S. scrofa* males gain most paternity in well-studied populations (Delgado *et al.* 2008; Hampton *et al.* 2004) this is not always the case (Spencer *et al.* 2005) and it remains to be tested whether sexual size dimorphism is less pronounced in populations where promiscuity and multiple paternity are observed.

We have demonstrated that sexual monomorphism in the collared peccary is coupled with polygynandry. The potential implications of these results for the co-evolution of body size, mating system and social behavior are intriguing. More data are needed on mate choice and parentage in this species to clarify how body size of both sexes may influence individual reproductive success. What we find most interesting about *P. tajacu* (and perhaps the peccaries in general) is the suite of morphological, grouping and behavioral traits departing from a single-male mating system based on resource defense polygyny (Emlen and Oring 1977), a departure for which we have now found genetic evidence.

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Figure Legends

Figure 1. Genetically sampled populations of wild collared peccary (*Pecari tajacu*) in the state of Texas (USA). Shading indicates average annual precipitation; from dark to light: > 122 cm, 91-122 cm, 61-91 cm, 30-61 cm, < 30 cm (data from United States Geological Survey, www.USGS.gov).

Table 1. Genetic diversity across microsatellite loci and frequency of inferred parentage assignments in three Texas populations of collared peccary (*Pecari tajacu*). One individual in the CWMA population reached maturity during the study.

	No. of loci	Mean no. alleles per locus	Mean H_E	Mean H_O	Mean proportion genotyped	N of immatures sampled	Assigned mother only	Assigned father only	Assigned both parents	% un-assigned
BB	10	6.2	0.68	0.64	0.97	48	9	11	25	6%
CWMA	10	5.8	0.66	0.65	0.99	42 (+1)	15	9	4	35%
WWR	11	5.6	0.60	0.64	0.86	9	1	1	0	77%

Table 2. Genetic relatedness and most likely family relationships among adults within herds in two populations of *P. tajacu* in Texas, inferred from multi-locus microsatellite genotype data. Average group size: BB = 10.4, CWMA = 10.2. *Lower bound (uncorrected for 50% sampling rate).

		Within-herd relatedness	No. same-sex adult parent/offspring	No. same-sex adult full sibs	No. same-sex adult half sibs	No. same-sex adult unrelated
BB	Males	0.25	0.9	0.5	1.2	1.5
	Females	0.26	1.7	0.5	1.6	2.1
CWMA	Males	0.18	0.2*	0.2*	1.0*	1.9*
	Females	0.23	0.8*	0.3*	0.5*	1.9*

Table 3. Most likely familial relationship between genetically related collared peccary (*Pecari tajacu*) dams and sires (BB population). Sequential ratio likelihood tests performed in ML Relate for putative against alternative familial categories (PO = parent/offspring, FS = full siblings, HS = half siblings, U = unrelated). Significance assessed over 10,000 iterations ($p < 0.05$).

Dam/Sire	PO - FS	FS - HS	HS - U	Pairwise r	Most likely relationship
BB003/BB014	0.46	0.42	0.01	0.27	HS
BB002/BB012	0.84	0.52	0.02	0.32	HS
BB009/BB014	0.67	0.46	0.01	0.35	HS
BB075/BB077	0.007	0.42	0.002	0.50	PO
BB085/BB084	0.39	0.007	0.01	0.51	FS

Table 4. No evidence for reproductive skew in female or male *P. tajacu* in Big Bend Ranch State Park, Texas. Shown here are the equal sharing values (the minimum B value possible through equal sharing of reproduction), lower and upper confidence intervals (CI); the observed B, and the reproductive monopoly value. The number of offspring attributed to males includes extra-herd paternity assignments. Power was assessed via simulation of B values over 5,000 iterations; depicted here is the likelihood of detecting skew in the observed herd (p<0.05).

Herd	Sex	No. adults	No. offspring	Equal sharing	95 % CI (lower)	B Obs	95 % CI (upper)	Monopoly	Power P (skew)
Agua Adentro	F	7	3	-0.29	-0.29	-0.10	0.37	0.57	0.23 (ns)
	M	8	1	-	-	-	-	-	-
Arroyo	F	4	2	-0.38	-0.38	0.38	0.38	0.38	<0.01
	M	6	7	-0.12	-0.12	0. 14	0.51	0.71	<0.01
Cinco Tinajas	F	3	2	-0.33	-0.33	-0.17	0.32	0.33	0.49 (ns)
	M	6	7	-0.12	-0.12	-0.06	0.13	0.71	0.28 (ns)
La Posta	F	2	3	-0.17	-0.17	0.33	0.33	0.33	<0.01
	M	2	0	-	-	-	-	-	-
Liebre	F	3	0	-	-	-	-	-	-
	M	2	3	-0.17	-0.17	0.33	0.33	0.33	<0.01

Lodge	F	2	7	-0.07	-0.07	-0.06	0.28	0.43	0.51 (ns)
	M	3	6	-0.11	-0.11	-0.06	0.32	0.56	0.46 (ns)
Monte	F	3	3	-0.22	-0.22	-0.22	0.23	0.44	<0.01
	M	3	4	-0.17	-0.17	0.13	0.49	0.50	0.20 (ns)
Pap. Colorado	F	3	3	-0.22	-0.22	-0.22	0.23	0.44	0.89 (ns)
	M	5	2	-0.40	-0.40	-0.10	0.39	0.40	0.51 (ns)
Solitario	F	8	2	-0.44	-0.44	-.063	0.43	0.49	0.50 (ns)
	M	6	1	-	-	-	-	-	-
West Oso	F	2	2	-0.25	-0.25	-0.25	0.24	0.25	0.50 (ns)
	M	2	0	-	-	-	-	-	-

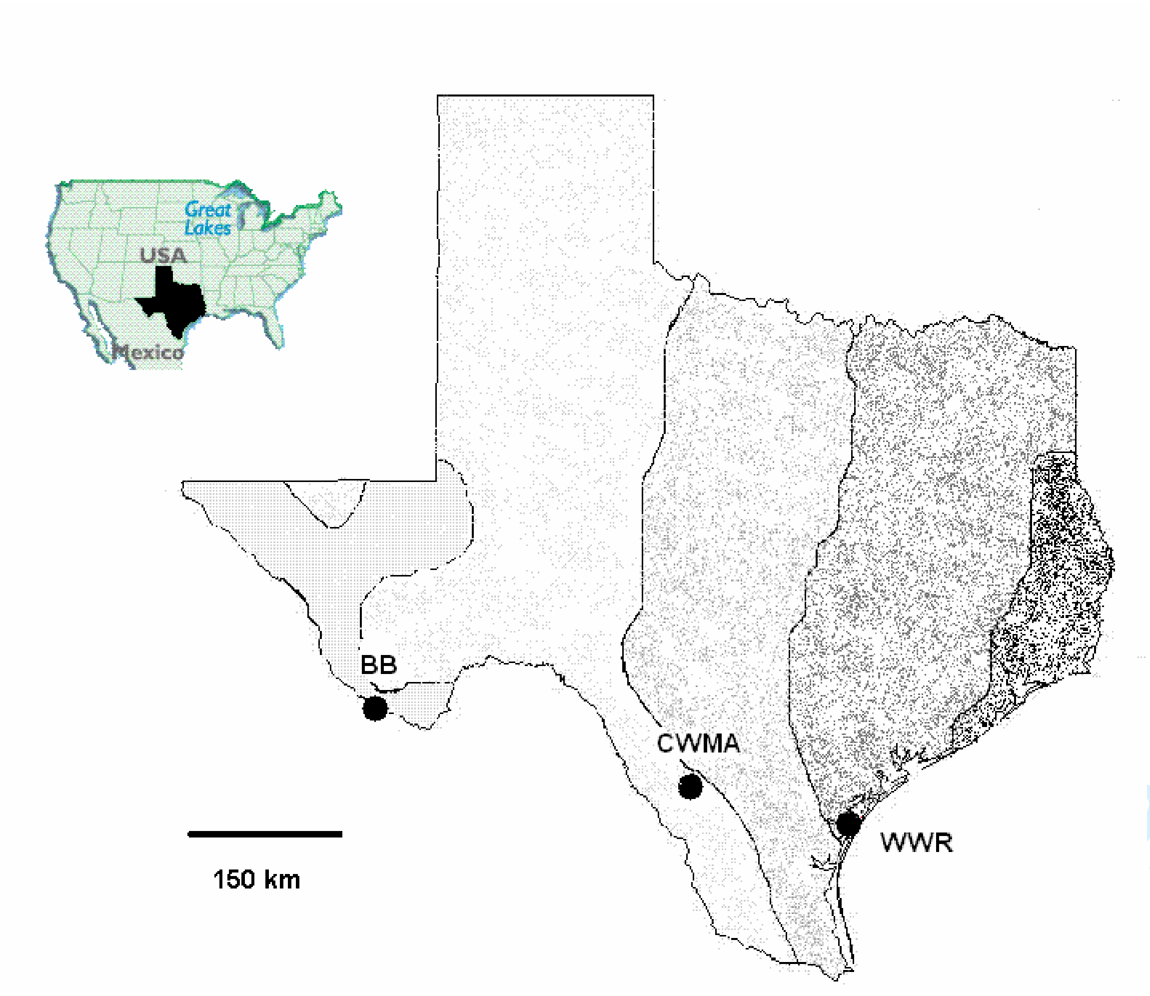

Fig. 1